THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

Vol. 88, No. 2 June 1976 Pages 185–376

PAIR-FORMATION DISPLAYS OF THE GREAT BLUE HERON

Douglas W. Mock

The Great Blue Heron (*Ardea herodias*) offers many advantages for the study of communication. It is large-bodied, conspicuous, fairly slow-moving, and geographically widespread across North America. Like many other herons it is rather solitary in habits through much of the year so its social behavior is concentrated into the breeding season. At that time herons aggregate in large nesting colonies where, with due caution, they can be observed at close range. Despite these advantages the published literature on Great Blue Heron social behavior consists of only 3 general accounts (Cottrille and Cottrille 1958, Meyerriecks 1960, Meyerriecks 1962). By contrast, the Old World Grey Heron, *A. cinerea*, has been extensively studied (Huxley 1924, Selous 1927, Holstein 1927, Verwey 1930, Strijbos 1935, Percy 1951, Lowe 1954, Owen 1959, Baerends and Baerends-van Roon 1960, Baerends and van der Cingel 1962, Hudson 1965, Milstein et al. 1970). This paper presents descriptions and illustrations of the social signals used by Great Blue Herons in the colony, including 6 displays previously undescribed for this species.

MATERIALS AND METHODS

Great Blue Heron reproductive behavior was studied for 2 breeding seasons in Minnesota and 2 breeding seasons in Texas. In 1970 and 1971 a 15-m scaffolding tower-blind was erected in a treetop heronry near Lino Lakes, Anoka Co., Minnesota (Lat. 45°10′N., Long. 93°10′W.). Daily observations were made through fledging for periods of up to 10 hours. Long-term observations were made in a colony on Hog Island, Redfish Bay, Aransas Co., Texas (Lat. 27°50′N., Long. 97°00′W.), in 1973 and 1975. The Texas herons built their nests on 1–3 m saltcedars (*Tamarix* spp.). A small shed (about 2m × 2.5m × 2m) was constructed in the center of the horseshoe-shaped colony with heron nests 10–15 m away on 3 sides. I lived totally inside this blind for 2–4 days at a time without disturbing the birds.

Observations of the nearest individuals and pairs were normally made through a

camera with an 8× telephoto lens. Written and dictated notes were augmented by several thousand still photographs plus approximately 300 m of super-8 movie film.

Both members of about 8 pairs (per season) were individually recognizable by facial plumage idiosyncracies (especially the irregular dark spots and smudge patterns on the anterior of the white forehead). These birds were scrutinized with a 60× spotting scope and sketched in an identification notebook. No artificial markings were needed. Sexes were identified on the basis of copulation position with the male assumed to take the top position (in pairs where several copulations were observed no reversals of position occurred).

In addition to qualitative descriptions, 30 hours of behavior sequences by Texas herons were dictated into a tape recorder and later plotted onto "timeline" sheets. The empirical data in this paper were derived from that sample. Temporal analyses of display function, made from these sequences, will be published elsewhere.

In this paper each signal will be treated separately in the following format: name, list of synonyms used by previous authors, description of a "typical" performance, observed variations, social contexts, and discussion. The discussion includes display design (sensory channels and morphological features that enhance transmission), "messages" (in the message-meaning system of Smith 1968: inferred primarily from contexts), evolutionary derivation from nonsignal motor patterns, and probable homologies in other species. Throughout the paper I use the term "homology" in the evolutionary sense, implying that the behavior was present in the common ancestor of the related species in which it is found today. Display terminology generally follows Meyerriecks (1960) except in the few cases where his names implied function or motivation (e.g., "Aggressive Upright" was renamed "Arched Neck"). Display names have been capitalized to distinguish them from non-social motor patterns (Moynihan 1955).

Breeding cycle chronology.—The Great Blue Heron's breeding cycle is similar to that of other herons (e.g., *A. cinerea*: Verwey 1930, Lowe 1954, Milstein et al. 1970) and will only be summarized here. The following chronological stages are my own convention:

(1) *Solo male stage.* An unpaired male heron chooses a site, usually containing an old nest, and defends it against all conspecifics. Typically such a solo male has seasonally bright-colored legs, lores, and bill (Meyerriecks 1960:104), but this is variable. Both in Minnesota and Texas populations the legs turn reddish, the irides develop a slightly deeper yellow, and the lores become bright cobalt-blue (see frontispiece), not lime-green as illustrated in Palmer (1962:366). The solo male displays "spontaneously" to the colony at large with no particular signal-receivers attending him.

(2) *Bachelor male stage.* I classify a male as "bachelor" when he has attracted one or more "satellite" females to his vicinity. His displaying then becomes oriented slightly more toward the attending female who approaches him hesitantly. If more than 1 satellite is present (maximum observed was 8), they may threaten one another; but generally they position themselves 3–10 m from the male and stand or preen. When a satellite female gets close to the male he performs agonistic displays and attacks, driving her away repeatedly. The bachelor stage is clearly a period of mutual assessment for the sexes: the male can reject the female by continuing to attack and she can reject him simply by leaving.

(3) *Paired stage.* Eventually the courting male allows 1 female onto his nest. The new alliance is very tense and ritualized Bill Duels erupt frequently. As the male's attack tendency wanes (over a span of several hours), mutual Bill Clappering increases. Copulations can occur any time after the female is accepted on the nest and are repeated

irregularly until the eggs are laid. During the first few days, the paired female spends most of her time away from the colony, presumably feeding. The male stays at the nest and defends it. When the mates are together on the nest they may loaf, perform displays, or engage in cooperative nest building (the male usually collects sticks and passes them to the female who inserts them).

(4) *Incubation stage.* Once the first egg is laid, male-female displaying decreases sharply. Incubation commences after the first or second egg (producing an asynchronous hatch), lasts 25–29 days (Pratt 1970), and is shared by both sexes. The nonincubating mate is usually absent, presumably foraging.

(5) *Parental stage.* After the eggs hatch, 1 adult broods the young chicks while the other hunts. Thus the 2 parents rarely interact and then only during nest-reliefs. When the chicks reach the age of 3–4 weeks their food demands peak, forcing both parents to hunt full-time to provision them. The youngest chick often starves to death by the 4th week. The parents' pair bond may weaken or disintegrate entirely by the time of fledging and independence of the young.

SOCIAL SIGNALS

Stretch

(1) *Synonyms*: *Reckbewegung* (Verwey 1930), Howling (Cottrille and Cottrille 1958), Bitterning (Milstein et al. 1970).

(2) *Typical performance.*—From a resting position with all feathers relaxed, the heron smoothly lifts its head and swings the closed bill toward vertical. During this ascent the lower neck plumes are fully erected, the scapular and occipital plumes relaxed, the torso inclines, and the head twists slightly to one side (Fig. 1: frames 0–63). At the peak (see frontispiece) the heron begins a long, moan-like call that continues through most of the descent. The hyoid apparatus can be seen moving beneath the tightly stretched skin of the throat. Descent begins as the legs flex at the "heels," the wrists move out from the body (about 6 cm), and the shoulders lower. During the descent the heron sways to the opposite side (and sometimes back again), as it shifts its weight from leg to leg. Neither crest nor scapular plumes are erected during the entire performance.

The Stretch lasts about 6 sec from start (when the bill is first lifted from horizontal resting position: Fig. 1, frame 0) to finish (the moment when the bill leaves its vertical apex: Fig. 1, frame 140). Mean Stretch durations for 2 males were 6.1 sec ($N = 21$, range = 4.5–8.3, S.E. = 0.21) and 5.5 sec ($N = 28$, range = 4.8–8.6, S.E. = 0.71).

(3) *Variations.*—The Stretch is probably the most stereotyped of Great Blue Heron displays, but there is noticeable individual variation. Each heron appears to have a distinctive form for its Stretch, so consistent that I learned to recognize individuals by display-form alone. For example, 5 of the 1975 Hog Island males were characterized as follows:

Male 2 — very little sway, no leg flex at all, downward motion of the bill

FIG. 1. Stop-action illustration of a complete Stretch. Each drawing was traced from movie film at 9-frame (½ sec) intervals. The vocalization began at frame 36; frontispiece position corresponds to frame 72. This individual does relatively little swaying or crouching in his Stretch.

only about 12 cm and due entirely to neck retraction, hyoid barely moves during call which is faint.

Male 15—all movements very stiff, no leg flex, body axis never dips below 25° above horizontal.

Male 16—at peak the bill passes vertical by 10–20° such that the heron is leaning over backwards slightly.

Male 18—choppy movements, performance ends suddenly after a very brief vocalization (sometimes no vocalization at all).

Male 20—unusually vertical body axis (never below 45°), legs flex deeply.

Components of the Stretch that show variation include: direction of the first lateral sway, amplitude of sway, angles of all axes (bill, torso, and legs), degree of neck-plume erection, speed and smoothness of performance, vocal characteristics (pitch, volume, duration, etc.), and degree of wing extension.

All herons, regardless of personal style, frequently give incomplete performances ("intention movements": Daanje 1950) of the Stretch. This usually consists of the bird raising its head as if beginning a full Stretch and then gently terminating the ascent after a second or 2 (to position of Fig. 1: frame 18). These intention movements are used in the same contexts as the full Stretch itself. They comprise 17% of the 850 Stretch performances in the timeline samples and become more common as the pairbond matures.

(4) *Contexts.*—The Stretch is performed in 4 distinct contexts, more than

any other Great Blue Heron display. It is the most common repertoire component of both solo and bachelor males. After pair-formation the Stretch is not discontinued as it is in many other heron species (e.g., Great Egret, *Casmerodius albus*: Wiese in press). It is given by a heron on the nest when its mate returns as part of the Nest Relief Ceremony and the Stick Transfer Ceremony. Finally, the Stretch is also used by the female when she has finished inserting one stick into the nest and is "sending" her mate off to collect another. Tomlinson (1974) briefly mentions the latter "sending off" context for the Stretch of the Purple Heron, *A. purpurea*, and Milstein et al. (1970) saw it 4 times in *A. cinerea*. It is in this "sending off" context that I most often saw the incomplete intention-to-Stretch functioning as a full Stretch. At first the male leaves the nest only after his mate does a full Stretch, but soon she begins abbreviating her performance. She repeats these intention-to-Stretch motions and mixes them with full performances until the male departs after the shortened version. Thus, the first phase of the Stretch display comes to replace the full performance as the mates get to know one another. Interestingly, in the Cattle Egret all female performances are abbreviated in form compared to the male's Stretch (Blaker 1969a: 86–87).

(5) *Discussion.*—The Stretch is the most conspicuous display in the Great Blue Heron repertoire. It also takes more time to perform than any other nonaerial display. The bright soft parts, especially the bill, are exhibited dramatically. The swaying motions are enhanced by the erection of the neck plumes. The wrists, normally tucked beneath a patch of black epaulet feathers, are held out revealing their chestnut lining. The accompanying vocalization calls attention to the visual effect and makes the display effective even at nightfall.

I believe that the Stretch encodes the messages of *identification* (probably individual), the *non-agonistic subset* ("I will not attack"), and the more general *bond-limited subset* in the message-meaning system of Smith (1969). In the solo male context the Stretch probably informs passing females of the male's availability for mating. During the bachelor stage it seems to be the invitation-to-approach that alternates with repelling attacks by the male. It is used in the paired stage in arrival situations when the mates are in close proximity to each other on the nest and attack tendencies are still high. In the fourth context, wherein the female apparently prescribes stick-collecting behavior for her mate, the message defies classification by Smith's scheme except in the loosely defined *bond-limited subset*. If this interpretation is correct, the signal probably facilitates cooperation between the mates in a shared task.

Various evolutionary origins of the Stretch have been suggested. Daanje

(1950) cited the Stretch of *A. cinerea* as a prime example of a ritualized intention movement (preflight take-off). Baerends and van der Cingel (1962) suggested that the display's form might be a mosaic of postural elements borrowed from conflicting drives to attack, flee, and settle-on-the-nest. In fact, herons show other motor patterns (e.g., the over-the-shoulder stick receiving posture of the female or certain active begging postures of nestlings) that bear as much physical similarity to the form of the Stretch as any published suggestion. Any of these hypotheses is plausible but, in my opinion, the origin of the Stretch is still an open question.

Homologous Stretch displays have been described for every member of the Ardeidae studied to date (see Blaker 1969a:87) except the Boat-billed Heron, *Cochlearius cochlearius* (Mock 1975a). Outside the family Ardeidae we should exercise great caution in suggesting Stretch homologies. Similar displays have been described for other members of the Ciconiiformes such as the White Stork, *C. ciconia* (Kahl 1972a), and the White Ibis, *Eudocimus albus* (Meyerriecks 1962). But equally similar-looking displays can be found in such unrelated taxa as penguins, albatrosses, gannets, ducks, gulls, terns, grackles, cowbirds, tits, and tanagers. Tinbergen (1959:62) notes that the abundance of bill-vertical postures in birds is surely complicated by convergence and he points out that there are a limited number of postures in which the primary weapon (bill) can be averted.

Snap

(1) *Synonyms*: *Schnappbewegung* (Verwey 1930), Bow-Snap (Milstein et al. 1970).

(2) *Typical performance.*—The plumes of the head, neck, breast, and back are erected as the head moves forward smoothly. When the neck is almost straight the heron suddenly flexes its legs at the "heels" and clacks its mandibles once loudly (Fig. 2).

(3) *Variations.*—The Snap is highly variable in form, involving neck angle, neck curvature, degree and distribution of feather erection, orientation of the display, leg flexion, twig-seizing, and lunging motions. The neck can be directed downward (as described above), upward, or anywhere in between. Low performances are by far the most common: of the 1352 Snaps in my timeline sample 72% had neck angles more than 20° below horizontal, 26% had neck angles between 20° below horizontal and 20° above, and only 2% had neck angles higher than 20° above horizontal.

Some of the higher Snaps resemble the Forward when they are performed without a vocalization (bill-clack only). Baerends and van der Cingel (1962) discriminated these 2 displays in *A. cinerea* on the basis of head orientation: high-neck performances facing conspecifics were considered Forwards, those

FIG. 2. Snap by Paired male as his mate watches (Hog Island, March 1973).

directed elsewhere were considered Snaps. This criterion generally fits my observations on *A. herodias* except that even low-neck Snaps are occasionally performed toward the receiver. The difference is probabilistic: Snaps *tend* to be done away while Forwards are always done toward the receiver. The importance of orientation is strongly suggested by performances that change

in direction during mid-Snap. I have also seen males turn their necks to one side so as to Snap with the body facing the receiver but the head diverted by 30°. Baerends and van der Cingel's orientation criterion offers no clarification in the case of rare voiceless performances that are aimed at nobody but still bear components of the Forward (rocking lunge and wings held far from the body). Overall I believe that the Snap and Forward are separate displays which share several components but that intermediates do exist.

Another display that occasionally mixes components with the Snap is the Arched Neck. I have seen horizontal Snaps performed with a well-curved neck in both Minnesota and Texas. This variant seems to come in bursts: an individual may do a dozen curved Snaps and then discontinue it entirely.

Snaps commonly include the brief grasping and shaking of a twig on the nest's bush. This stifles the audible bill-clack and seems to intergrade with the form of yet another display, the Twig Shake. Usually Snaps that include twig-grasping are done much more gently and seem to follow bouts of stick manipulation. Meyerriecks (1960:99) also described a variant he termed the Low Bow which I have seen in neither Minnesota nor Texas.

Individualistic variations are not so marked in the Snap as in the Stretch though certain individuals seem to prefer low Snaps and others perform with little or no leg flexing. A sample of 75 Snaps by one Texas male showed that 68% of his performances were accompanied by strongly bent legs, 22% by moderately bent legs, and 10% by straight legs. In plumage 86% had full head and neck erection, 10% had moderate erection, and 4% had no erection at all.

(4) *Contexts.*—The Snap is a major part of the male's display repertoire during the solo and bachelor stages. After pair-formation it decreases quickly and is nearly absent by the time of egg-laying. Neither the form nor frequency of the Snap changes noticeably between the solo and bachelor stages.

Females perform Snaps too, but much less often than males. My timeline samples show 415 Snaps during the bachelor stage, of which 97% were performed by males; during the paired stage males performed 83% of the 291 total Snaps. This agrees with the data for *A. cinerea*: of 1977 Snaps, males did 96% (Baerends and van der Cingel 1962). Meyerriecks (1960:99) thought that *only* male Great Blue Herons did Snaps but he was not studying recognizable individuals. Snaps of males and females are very similar in form but females seem to prefer the horizontal neck angle, less leg flexion, and may be a little slower in overall performance.

(5) *Discussion.*—If a full spectrum of Snap variations were plotted, ranging from twig-grasping performances (resembling unritualized nest-building) on

one end and upward performances (resembling voiceless Forwards) on the other, the frequency distribution would be strongly unimodal at the "typical" low-necked Snap described above. But the atypical performances raise the possibility that the variability is conveying additional information. Because the variability is present in a continuum (with all intermediates) it can be considered "graded" in form.

The overall function of the Snap is difficult to assess. It is used in all contexts of courtship, with or without females attending, suggesting that it is a general advertisement, perhaps analogous to the territorial song of male passerines: it probably attracts unmated females and repels males. Approaching satellite females show little or no overt response to a male's Snap.

The Snap is thought to have evolved from fish-seizing (Verwey 1930), twig-grasping during nest-building (Meyerriecks 1960), or as "the direct result of the instincts activated" (namely "... to attack, to flee, and to settle down ...," Baerends and van der Cingel 1962). I favor Meyerriecks' view that the Snap evolved from twig-grasping and has been ritualized to the point of ignoring the stick in most, but not all, performances. It is possible that the upward performances are functionally and evolutionarily distinct from the more typical low Snaps and should be considered as variants of the Forward.

Homologous displays have been reported for every heron studied except the night-herons (Voisin 1970, Nelson 1975, Mock 1975a) and the Cattle Egret (Blaker 1969a, Lancaster 1970).

Wing Preen

(1) *Synonyms*: Wing Touch (Blaker 1969a), *Lissage des Plumes* (Voisin 1970), Wing-stroke (Wiese in press).

(2) *Typical performance.*—The heron leans forward, moves 1 wing a few cm down and out from the body, then runs its bill smoothly along the leading edge of the primaries (Fig. 3). This stropping motion is often repeated a second time before the heron resumes a standing position. The entire performance takes 2–4 sec. When doing Wing Preens herons usually orient themselves broadside to the signal receiver (80% of 142 performances in a sample); from that position they tend to choose the wing closest to the receiver (68% of the 113 broadside performances)—both these tendencies are statistically significant (χ^2 test, $P < .001$).

(3) *Variations.*—Wing Preens vary in stroke number, stroke placement, stroke length, and spatial orientation relative to the receiver. Usually there is either 1 stroke (55% of 620 Wing Preens in sample) or 2 strokes (40%), but performances of 3 or 4 strokes occur also (< 5% combined). While stroke number does not change significantly through the chronological stages

Table 1

Individual Differences in Number of Wing Preen Strokes for 4 Male Great Blue Herons (Hog Island, 1975)

Male	1-stroke	2-strokes	N
A	18%	66%	38
B	66%	32%	111
C	76%	24%	37
D	81%	19%	43

of pair-formation, certain individuals do show preferences for single-stroke and others for double-stroke Wing Preens (Table 1).

The tip of the bill, though typically passing along the wing's leading edge, sometimes runs several cm above that or even among the primary coverts. Occasionally it is even performed without touching the wing at all, merely sweeping parallel to the edge. Sometimes the bill chews at feathers during the display and may even pause while nibbling. Incomplete strokes are also quite frequent.

(4) *Contexts.*—The Wing Preen is a basic component of the male display repertoire throughout pair-formation. It is also performed by females but much less frequently: of the 513 Wing Preens sampled when both sexes were present (bachelor and paired stages), only 123 (24%) were done by females. Generally, Wing Preens can occur at any time that the male is displaying on his nest. It is one of the "spontaneous" displays used throughout pair-formation.

(5) *Discussion.*—As far as I know the ritualized Wing Preen has never been described before for an *Ardea* species. The oversight of previous workers can be readily understood in light of the similarity between this display and the normal preening motions from which it doubtlessly evolved. Once aware of it, however, I had no trouble distinguishing it: the heron always holds its wing the same way, preens it 1 or 2 strokes, and sometimes actually fails to touch it at all.

Once the Cattle Egret's Wing Preen was first described by Blaker (1969a) it has been found in many other species including: Great Egret (Wiese in press), Louisiana Heron (*Hydranassa tricolor*: Rodgers in press), Little Egret (*Egretta garzetta*: Blaker 1969b), Yellow-billed Egret (*E. intermedia*: Blaker 1969b), Snowy Egret (*E. thula*: pers. obs.), Little Blue Heron (*Florida caerulea*: pers. obs.), Black-crowned Night Heron (*Nycticorax nycticorax*: Voisin 1970, Nelson 1975), and possibly Boat-billed Heron (Mock 1975a). Somewhat similar displays also occur in the storks: Kahl (1972b) described Display Preening in the tribe Mycteriini.

FIG. 3. Wing Preen: male runs his bill-tip along the leading edge of his wing as his mate ignores him (Hog Island, March 1973).

The function of the Wing Preen is hard to assess. Its performance by courting unpaired males, approaching females, and members of newly-formed pairs suggests that it plays a role in pairbond formation but specific responses to the display's performance are not readily observable. The posture of the display, especially the directing of the bill toward the sender's own body, suggests Smith's (1969) *non-agonistic subset* ("I will not attack") which I suspect to be one of its messages.

Circle Flight

(1) *Synonyms*: circling nuptial flight (Selous 1927), Courtship Flight (Milstein et al. 1970).

(2) *Typical performance.*—Instead of retracting its neck against the shoulders as in normal flight, the heron keeps its neck fully extended throughout (Fig. 4) as it flies in a large (usually 50–75 m diameter) circle, ending back near its origin. The wingbeats are slightly slower and deeper than normal, producing an audible "whomp" with each stroke. The Circle Flight requires more time than any other display. Ten male performances ranged from 15–30 sec ($\bar{x} = 22.2$) and 8 female performances ranged from 16–50 sec ($\bar{x} = 28.1$).

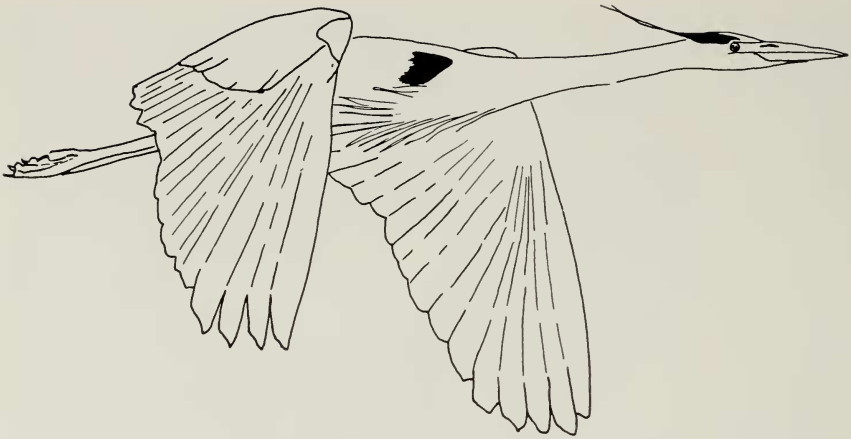

FIG. 4. Straight-necked flying position of the Circle Flight.

(3) *Variations.*—The Circle Flight is extremely variable in shape of flight-path, size of the circle flown, duration, and details of landing. Some flights have 2 laps instead of 1, some have a figure-8 pattern, and one was observed in which a male carried a stick in his bill. Wind conditions and heron traffic over the colony probably affect many flights.

One newly-paired male completed a Circle Flight by landing on his mate's back where he unsuccessfully attempted to copulate (she resisted by pecking at him). Female Cattle Egrets use the Circle Flight as a mounting tactic to subdue courting males (Lancaster 1970).

(4) *Contexts.*—In general, the Circle Flight is uncommon for either sex. Unpaired males normally use their nest-territory for both takeoff and landing but they occasionally use Circle Flights to move to an alternate display site (e.g., a vacant nearby nest). Satellite females tend to land closer to the courting male each time they do a Circle Flight: it serves as an approach technique. The final move onto the male's nest is sometimes achieved via a Circle Flight. During the first days of the pairbond, both sexes continue to perform infrequent Circle Flights.

On certain mornings Circle Flights are unusually frequent for the colony as a whole. This may be due to a form of display imitation ("social facilitation") or it may simply indicate that extrinsic conditions, especially wind, are especially suitable for aerial displaying.

(5) *Discussion.*—The Circle Flight has not been previously described for the Great Blue Heron though Meyerriecks (1960:102) suspected its existence. It has been noted in *A. cinerea* (Selous 1927, Verwey 1930,

Milstein et al. 1970), Great Egret (Wiese in press), Louisiana Heron (Rodgers in press), Snowy Egret, Reddish Egret (*Dichromonassa rufescens*), Green Heron (*Butorides virescens*) (Meyerriecks 1960), Cattle Egret (Blaker 1969a, Lancaster 1970), Little Egret and Yellow-billed Egret (Blaker 1969b). Meyerriecks noted that the small-bodied herons tended to perform more aerial displays than large-bodied herons. The infrequency of Great Blue Heron Circle Flights supports this idea: it comprises only 11% of the satellite female's meager display repertoire, 0.4% of the male's bachelor repertoire, and even less after pair-formation.

The functions of the Circle Flight seem to change in the different contexts. For solo and bachelor males it probably conveys the messages of *identification* and *locomotion* (Smith 1969). Like the other heron advertisement displays I suspect that the identification message provides quite detailed information on sex, species, and general vigor of the sender. Satellite females presumably use this information in deciding which males to approach. Circle Flights by satellite females, while giving that same kind of information to the males, also bring them physically closer to the nest. The fact that it is used in this manner suggests that the Circle Flight also carries an appeasement message (Smith's *non-agonistic subset*). Within the context of the new pairbond the Circle Flight may acquire a social-cohesion message (*bond-limited subset*: Smith 1969).

Landing Call

(1) *Synonyms*: Greeting call (Cottrille and Cottrille 1958), Alighting Display (North 1963, Milstein et al. 1970), Rick-rack (Blaker 1969a), Greeting Display (Rodgers in press).

(2) *Typical performance.*—When landing at its nest the heron fully extends its neck, erects its crest, and emits a series of low-pitched croaking notes. The call usually begins when the bird is braking about 10 m from the nest, and continues at 1-sec intervals until it lands.

(3) *Variations.*—The structural qualities of the Landing Call have not been recorded and studied in detail but I have the impression that there are considerable differences in pitch and tone and that these differences may be individualistic. Some notes are monosyllabic ("rok-rok-rok . . .") but most are di-syllabic ("arre-arre-arre . . .").

(4) *Contexts.*—Great Blue Herons use the Landing Call almost every time they land on the nest throughout the breeding season, especially if a mate is already present. Parents give it as they return to the nest to feed their chicks.

(5) *Discussion.*—The Landing Call has been described only as a part of the complex Greeting Ceremony and never as a complete display in itself. I

treat it as such because it includes a vocalization, it has a crest-raising component, and it occurs in social contexts.

I believe that the Landing Call provides information on individual recognition and announces the heron's arrival: Smith's (1969) messages of *identification* and *locomotion.* Mate-recognition is even possible to observe in the colony because non-mates who make the error of landing at the wrong nest are immediately attacked and driven away. I believe that Great Blue Herons can distinguish their mates at distances of at least 100 m: I have watched incubating herons rise suddenly, turn, and stare at an approaching mate long before it could have received an acoustic signal. It seems, therefore, that members of a mated pair are attuned to very subtle differences in flying motions. At closer distances the Landing Call serves to get the mate's attention if it has not been watching in the right direction. This recognition system is presumably important for a large, potentially dangerous bird like a heron that must coexist with its mate on a restricted nest site (see Nelson 1967 and 1971). The vegetation structure and spacing of nests usually obviates the simpler option of landing first, getting the mate's attention, and then proceeding to the nest. Similar vocal recognition has been demonstrated with play-back experiments for the colonial Northern Gannet (*Sula bassana*) which also nests in crowded colonies (White 1971, White et al. 1970).

Highly ritualized landing displays are present in other ardeid species such as Great Egret (Wiese in press), Snowy Egret (pers. obs.), Louisiana Heron (Rodgers in press), and Boat-billed Heron (Mock 1975a). Some of these are similar to the Great Blue Heron's Landing Call and may be homologous.

Twig Shake

(1) *Synonyms*: Twig Quivering (Baerends and van der Cingel 1962).

(2) *Typical performance.*—The heron extends its neck slowly, grasps a branch in its mandibles, and shakes it side-to-side or forwards-and-backwards. There are no accompanying vocalizations as found in the Twig Shake of the Cattle Egret (Blaker 1969a).

(3) *Variations.*—Many aspects of the Twig Shake show variability, including vigor of performance, orientation relative to the receiver, duration, neck angle, feather erection, grip, and choice of the twig. Usually the twig is part of the tree supporting the nest (in only 5% of 291 cases was the nest itself involved) and it is usually too thick or flexible to be broken off and added to the nest. Similar "tremble-shoving" movements, used when inserting a stick into the nest, are much gentler and longer in duration than the Twig Shake, which normally lasts only 1–3 sec.

As in the Snap, the neck angle in the Twig Shake can range from about 60° above to 60° below horizontal. Unlike the Cattle Egret (Blaker 1969a)

the vast majority of Great Blue Heron Twig Shakes (95% of 291) are below horizontal.

The most conspicuous variability in the Twig Shake is in overall vigor of performance. Speed and amplitude range from gentle trembling to wild thrashing that can even cause the heron to lose its balance. This latter type of Twig Shake (collectively called *vigorous*) tends to replace the non-vigorous performances in social contexts (e.g., when a female approaches a displaying male). Thus the *vigorous* form accounted for only 32% of all solo male Twig Shakes (N = 114) but increased to 50% during the bachelor stage (N = 100) and 57% during the paired stage (N = 77).

Other variants of the Twig Shake include performances in which the stick is nibbled on (resembling the mandibulations of Bill Clappering). As mentioned earlier, a few very low performances intergrade with variants of the Snap and are virtually impossible to assign to either category.

(4) *Contexts.*—The Twig Shake is most commonly performed by the male: of 191 Twig Shakes recorded with both sexes present only 7% were done by females. The display is often given "spontaneously" by solo males (non-vigorous form) but increases in frequency when the male is being approached by a satellite female and when both sexes are first co-occupying the nest. At these times the male seems very nervous and excited and *vigorous* Twig Shakes predominate.

(5) *Discussion.*—The Twig Shake is not highly ritualized but I believe that it should be considered a display because the sticks involved are almost always inappropriate for nest-building purposes. The variability found in the Twig Shake's form may enable it to carry a large amount of "graded" information: because the *vigorous* forms appear under different social contexts from the non-vigorous forms, different information is probably being conveyed. *Vigorous* performances may well express redirected aggression.

The Twig Shake presumably evolved from nest-building motor patterns which it still resembles. It is probably homologous with the little-ritualized Twig Shakes of the Cattle Egret (Blaker 1969a, Lancaster 1970) and Boat-billed Heron (Mock 1975a) and may represent the primitive condition from which more highly ritualized displays evolved in the Great Egret (Bow: Wiese in press) and Black-crowned Night Heron (Twig Ceremony: Noble et al. 1938).

Crest Raising

(1) *Synonyms*: None.

(2) *Typical performance.*—The heron erects its black and white occipital plumes to a variable degree for a few seconds and relaxes. Displaying herons usually turn toward the stimulus that elicited the performance.

(3) *Variations.*—The form of Crest Raising varies continuously ("graded" in form) with respect to angle of erection, duration, orientation, and even the feathers raised. As Blaker (1969a) noted for the Cattle Egret, the anterior and posterior portions of the Great Blue Heron's crest can be erected independently.

(4) *Contexts.*—Crest Raising is both a signal performed by itself and one that is incorporated into other displays. Great Blue Heron displays which include a Crest Raising component are: Snap, Landing Call, Arched Neck, Forward, Supplant, Bill Duel, *Hard* Contact Bill Clappering, and *vigorous* Twig Shakes.

By itself, Crest Raising is performed by both sexes throughout the breeding season and is also used outside the colony on the foraging areas. Solo males seem nervous when they first claim a nest; they show Crest Raising in response to many stimuli (passing conspecifics, sudden noises, etc.). The display is most frequently used later, as a short-range signal between the sexes during pair-formation. At that time females perform Crest Raising about twice as often as males: they are reacting not only to their prospective mates but also to the same stimuli that elicited Crest Raising in solo males. New mates seem very nervous and commonly perform Crest Raising as a response to each other's movements. Female Crest Raising, when accompanied by head-elevation, quickly triggers male Bill Duel attacks at this time (see p. 210).

Great Blue Heron nestlings can perform Crest Raising by the age of 2 weeks (pin feathers of the head are about 1 cm long). They show it in response to a wide array of nest disturbances (e.g., parent landing on the rim) and as a component of the Forward.

(5) *Discussion.*—The optical effect of Crest Raising by adult Great Blue Herons is greatly enhanced by the contrast of a 2-tone crest. From the front a white-on-black pattern is produced when the full crest is erected and a white-only signal when the anterior portion is raised by itself. Accurate measurement of the possible message differences between these 2 signals was not attempted in this study. If Crest Raising *does* carry graded information its role as a component of 8 other Great Blue Heron displays should be re-evaluated. Conceivably it could modify all those messages and thereby greatly enrich the entire communication repertoire.

Crest Raising has been described, either as a separate display or as a component of other displays, in every ardeid species studied to date. It even occurs in the Great Egret which lacks specialized occipital plumes (pers. obs.).

All feather erection signals probably evolved initially from autonomic

FIG. 5. Female assumes Fluffed Neck as her mate brings a stick to the nest (Hog Island, March 1973).

responses promoting convection cooling (Morris 1956). Any visible autonomic response that reliably precedes (and therefore predicts) exertion can be selected for its communication function (Andrew 1972:194). In the case of feather erection the resulting increase in apparent body size presumably

also contributed toward its evolution as a threat signal (Darwin 1872, Meyerriecks 1960).

Fluffed Neck

(1) *Synonyms*: Stiff-necked Upright Display and Aggressive Upright Display (Meyerriecks 1960), Erect Stance (Wiese in press), Aggressive pose (North 1963: fig. 5), and Upright (Rodgers in press).

(2) *Typical performance.*—The heron elevates its head to about ¾ maximum height and erects all the neck feathers to an extreme degree. The bill is usually open about 2 cm at the tip (some performances include a soft vocalization) and is either horizontal or slightly inclined (Fig. 5). The head may be drawn back slightly. The unique features of the Fluffed Neck are the horizontal angle of the bill and the extreme feather erection that encompasses the entire neck, not just the basal plumes as in most other displays.

(3) *Variations.*—The Fluffed Neck shows variability in the degree of vertical neck extension, the angle between the neck and bill, the erection of the occipital crest, and the vocalization.

(4) *Contexts.*—Great Blue Herons perform Fluffed Necks in 2 different contexts. It is used most commonly by paired females during cooperative nest-building. As the male repeatedly brings sticks to the nest the female sometimes greets him with the Fluffed Neck instead of the more usual Stretch or Arched Neck. I have also seen a heron give the Fluffed Neck when a Laughing Gull (*Larus atricilla*) swooped at it.

The Fluffed Neck is very rare in the Great Blue Heron but in the Great Egret it is the typical greeting signal between mates and is a general threat to others (Wiese in press). Displays that I consider as homologous with the Fluffed Neck have been described for a number of other heron species—unfortunately, under a confusing maze of synonyms. On the basis of display form, I recommend that Fluffed Neck, Arched Neck, and Upright displays be clearly distinguished (Table 2).

Upright

(1) *Synonyms*: None.

(2) *Typical performance.*—The heron raises its head forward and up until the neck and bill are very straight, pointing about 45° above horizontal. The crest may be either erect or sleeked. The heron holds this position for up to about 4 sec and then relaxes (or attacks).

(3) *Variations.*—Through variation in the angle and straightness of the neck, the Upright seems to grade into Arched Neck postures (see p. 204).

TABLE 2

CHART OF PROPOSED FLUFFED NECK HOMOLOGIES AND KEY TO SYNONYMS



	Arched neck	Fluffed neck	Upright
Ardea cinerea	Aggressive Display[2]		
A. herodias	Aggressive Upright[3]	Fluffed Neck[8]	Upright[3]
A. melanocephala		Aggressive Pose[5]	
Casmerodius albus		Erect Stance[7]	Upright[7]
Egretta thula		Aggressive Upright[3]*	
Hydranassa tricolor		Upright[6]	
Dichromonassa rufescens		Aggressive Upright[3]*	
Butorides virescens		Stiff-necked Upright[3]	
Bubulcus ibis		Upright[1]	
Nycticorax nycticorax		Ruffle Neck[4]	

1 = Lancaster 1970, 2 = Lowe 1954, 3 = Meyerriecks 1960, 4 = Nelson 1975, 5 = North 1963 (fig. 5), 6 = Rodgers in press, 7 = Wiese in press, 8 = present paper. (*Meyerriecks' original descriptions indicate that the "Aggressive Upright" and the "Upright" intergrade as escape/attack tendencies vary—in lieu of further published detail I prefer to treat these as one variable display.)

In addition, the degree of crest erection is highly variable and the wings may be held several cm out from the body.

(4) *Contexts.*—I have seen the Upright only a few times in the colony, always in contexts similar to those of the Arched Neck when a conspecific lands nearby or flies close by.

(5) *Discussion.*—I have observed this display so infrequently that I initially considered it to be a minor variant of the Arched Neck. Meyerriecks (1960:94), however, in describing it for the Great Blue Heron said that it "... is most commonly seen where large numbers of *herodias* are feeding in close proximity . . . ." He also observed it during the "dancing ground" activities (see p. 223). Thus it may well be a distinct signal used primarily in special circumstances away from the colony.

This posture has been described as an agonistic display in several other heron species. It is a common colony display in the Great Egret (Wiese in press) but Meyerriecks' (1960) descriptions for the Reddish and Snowy egrets do not strongly resemble the oblique posture that I label as Upright: they sound very similar to my Fluffed Neck.

Arched Neck

(1) *Synonyms*: Aggressive Display (Lowe 1954), Aggressive Upright Display (Meyerriecks 1960), Arched-neck Greeting Display (Milstein et al. 1970).

(2) *Typical performance.*—Quickly the heron erects its plumes (crest, scapular, and basal portion of the neck) and curves its neck like a rainbow so that the closed bill usually points below horizontal (Fig. 6). It maintains this position up to 5 sec before relaxing to a standing posture.

(3) *Variations.*—The greatest sources of variability in the Arched Neck are the degree of neck curvature, degree of feather erection, and directional orientation of the performer. It is possible that individual herons perform consistently with respect to neck curvature. Occipital crests were sleeked during about ¼ of 272 male Arched Necks, but this variant was observed only once in 63 female performances. Furthermore, the males' sleeked variant virtually disappears after pair-formation (only 4% of all Arched Necks).

Less common variations include Arched Necks given from an incubating crouch, repetitions given quickly (even 1 triple performance), and 2 performances that included rocking stab-like motions resembling the Forward. The Arched Neck is ordinarily a noiseless display but one particular male added a grunt-like vocalization during some of his performances.

(4) *Contexts.*—Arched Necks usually occur in response to the movements of other herons in the colony—birds that are walking, landing, departing, or more commonly, just flying past. A heron landing within 2 to 10 m usually elicits an Arched Neck: herons landing farther away are mostly ignored: herons landing closer are typically attacked. Following an Arched Neck the performing heron either gives a Forward or Supplant (if the landing was close by) or relaxes (if the landing was farther away). When the moving heron is not landing but is merely flying low over the colony, the Arched Neck may be elicited at greater distances (up to 20 m).

Arched Necks are also performed in response to non-heron stimuli such as sudden loud noises (e.g., gunshot, boat-motor) or a human approaching the heronry. At these times many colony members may display simultaneously (Fig. 6), but each seems to be responding directly to the external stimulus rather than to other herons.

Although performed by both sexes during pair-formation, Arched Necks are given most frequently by unpaired males standing on their own nests. Satellite females begin doing it only when they have approached the male very closely; their usage then increases after the pairbond has formed. Thus, in the colony, the Arched Neck is closely associated with nest-territory ownership. Away from the colony it is used as a spacing signal on the "gathering ground" (see p. 223).

FIG. 6. Simultaneous Arched Necks given by bachelor male and satellite female as conspecific flies past. Note that male's crest is more erect than female's (Rice Lake, April 1971).

After pair-formation, Arched Necks are used irregularly during the arrivals and departures of both sexes, especially in the first days when both mates are still nervous around each other. It is usually followed by Bill Clappering.

(5) *Discussion.*—In contrast with the displays already described, the Arched Neck's context can be much more narrowly defined: it is almost always elicited by a moving heron. I believe that the Arched Neck functions as a relatively long-distance threat whose message (*attack*) might be paraphrased as "Keep your distance." This idea is supported by the fact that Arched Necks are most frequent during the early phases of the breeding cycle when the herons are defending new territories and are crowding into the colony for their first sustained social contact in months.

The Arched Neck probably evolved from a standing alert posture. It has been reported only for the first 2 species of Bock's *Ardea* superspecies (*cinerea–herodias–cocoi*: Bock 1956). It is also possible that the Arched Neck evolved as a variant of the ancestral Fluffed Neck (which I assume to be ancestral because that character-state is much more widely shared) that

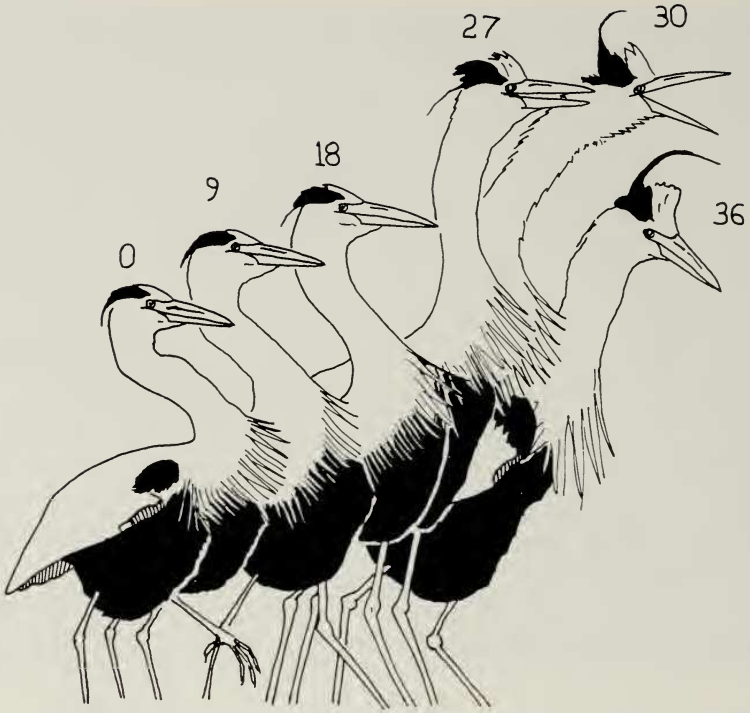

FIG. 7. Stop-action illustration of the Forward (from movie film shot at 18 fps). Frame numbers are given over each figure.

proved more effective/successful in evolutionary competition among signals (Moynihan 1970). Observations on other species of *Ardea* (especially *A. cocoi*) are needed to determine the taxonomic distribution of this display.

Forward

(1) *Synonyms*: *Stossbewegung* (Verwey 1930), Threat Display (Cottrille and Cottrille 1958), Forward Display and Full Forward Display (Meyerriecks 1960), Bill-snapping and Threat Display (Milstein et al. 1970), *La Menace* (Voisin 1970), Upward Snap (Birkhead 1973).

(2) *Typical performance.*—The heron moves its wrists out from the sides of the body, retracts its neck part way onto the shoulders, and erects all plumes of the head, neck, and back. In this position it either stabs at another bird or walks toward it before stabbing. The stab is performed with a rocking motion: the legs straighten, the neck extends, and the head passes

FIG. 8. Forward given by 3–4 week old chick (Danger Island, Texas, May 1974).

through a short arc as the heron emits a sharp "squawk" and clacks its bill at the point closest to its opponent (Fig. 7). After a Forward the heron pauses and, if the other bird has not moved away, it often repeats the Forward or continues advancing. On rare occasions the displaying heron gets close enough to make contact during the stab.

(3) *Variations.*—Almost everything about the Forward is variable—crest erection, walking motions, wing position, qualities of the call, etc. As described under the Snap, voiceless performances of the Forward are sometimes difficult to distinguish from high Snaps and are considered a distinct display, Bill-snapping, by Milstein et al. (1970).

(4) *Contexts.*—Forwards are usually performed from the nest as part of territorial defense. Solo males begin using it as soon as they have chosen a nest-site. Bachelor males do the most Forwards (in repelling satellite females) and paired males do relatively few. Female herons perform fewer Forwards than males and direct them primarily toward other satellite females during the bachelor and paired stages.

Less commonly, Great Blue Herons of both sexes direct Forwards at nearby commotions. These are usually social (e.g., neighbors fighting), but can actually be any heron-caused disturbance, such as a clumsy landing. Local arrivals typically elicit Arched Necks followed by Forwards. Forwards can be directed at herons up to 15 m away, but are usually used in closer situations (8 m or less).

Great Blue Heron chicks perform recognizable Forwards toward siblings when only a few days old. As time passes they use the Forward (and actual pecking) to repel competitive siblings at feeding times and, by the age of 2–3 weeks (Fig. 8), the chicks can defend the nest against conspecifics (wandering neighbor chicks and stick-stealing adults) and perhaps against certain predators (e.g., gulls and night-herons). Forwards by chicks tend to lack the vocal component, terminating most commonly in a loud bill-clack (as reported for *A. cinerea* by Baerends and van der Cingel 1962). The frantic competitive begging that occurs each time a parent returns with food usually includes many Forward-like lunges at the parent: apparently chicks attack everything in their environment and this attack behavior elicits a regurgitation response from the parents.

(5) *Discussion.*—The Forward is one of the few heron displays in which the signal's receiver is seldom in doubt. I felt that I could determine the receiver in 99.4% of 349 Forwards. The identity of the receivers changed through the pairing process, from any passing conspecific in the solo male stage to satellite females in the bachelor male stage and back to any passing conspecific in the paired male stage (Fig. 9).

The Forward is apparently a ritualized attack posture derived from the intention movement to deliver the blow. It has been described for all heron species studied to date with the only questionable homologies being the An-Snap of *Cochlearius* (Mock 1975a) and the *Pfahlstellung* of *Botaurus* (Portielje 1926).

The Forward conveys a strong *attack* message which can be represented as "Move away!" This function is served by the extreme conspicuousness of the overall display (visual and acoustic) and presumably by all the size-increasing components (feather erecting, wing-lifting, and physical advancing). The bill, which is the heron's primary weapon, is held foremost and is brightly colored during pair-formation.

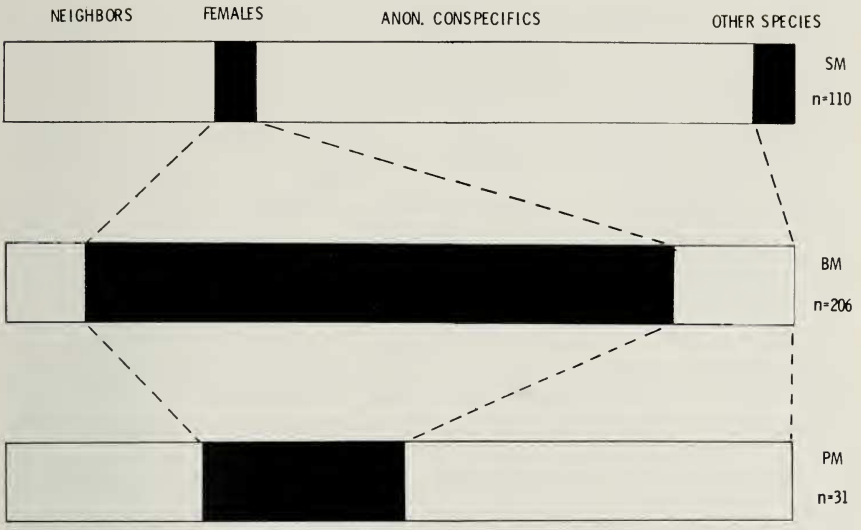

FIG. 9. Identity of receivers for 347 Forwards given by male Great Blue Herons throughout pair-formation. Each bar represents 100% of the Forwards for its pairing stage: SM = solo male stage, BM = bachelor male stage, PM = paired male stage.

Supplanting

(1) *Synonyms*: Supplanting Run (Blaker 1969a), *L'Attaque* (Voisin 1970).

(2) *Typical performance.*—The attacker flies directly at another heron, erecting all feathers and emitting a loud squawk. If the opponent does not flee it is landed on and pecked. Usually the attacker lands on the spot just vacated by its opponent, stands there for a variable period slowly relaxing its plumes, and then returns to its original perch.

(3) *Variations.*—Even more than the Forward, this display varies in all details, depending on such additional things as the distance flown and the opponent's reactions.

(4) *Contexts.*—Supplanting is seen most commonly when a satellite female has either come too close to a bachelor male's nest or has failed to move away after several Forwards by the male.

(5) *Discussion.*—Supplanting differs from totally unritualized attack only by the presence of a vocalization. The *attack* message is obvious and is immediately reinforced by the signaler's action. Similar flying attack signals have been reported in most other species. There is some doubt in my mind about whether Supplanting should be maintained as a display separate

FIG. 10. Bill Duel. Male stabs at female's open bill while she recoils and tries to catch his bill. Female succeeds in catching male's bill: the Duel ends in a clinch (Hog Island, March 1975).

from the Forward. I have distinguished the 2 solely on the basis of flying locomotion.

Bill Duel

(1) *Synonyms*: bill-sparring (Lowe 1954, Cottrille and Cottrille 1958, Meyerriecks 1960), inhibited mutual bill fighting (Baerends and van der Cingel 1962), stab-and-counterstab (Blaker 1969a).

(2) *Typical performance.*—If a newly-paired male sees his mate raise her head above her shoulders he usually attacks in a ritualized manner. He quickly erects all plumage (especially crest and neck), stands very tall, and then lunges at her face with wings held out and bill closed. The female avoids the stab by quickly retracting her neck so that his thrust ends just short of contacting her bill-tip (Fig. 10 left). Then the male retracts his neck for another stab and the female moves her head back to a normal position, watching him closely. This cycle of male stabbing and female pulling back often continues for about 4 repetitions, producing a seesaw action between the mates. The female usually keeps her bill open when the male thrusts

FIG. 11. Female (left) averts her bill when standing close to her new mate (Hog Island, March 1973).

and tries to seize his bill in the tips of her mandibles. If she succeeds and can hold on, she can end the Bill Duel in a clinch (Fig. 10 right). Bill Duels last 1–5 sec, depending on the number of male stabs and whether or not the female catches his bill-tip.

(3) *Variations.*—Because this mutual display has so many variable com-

ponents, it is simpler to discuss the common features of all Bill Duels which qualify it as a display and make it recognizable. First of all, it is almost always started by the male of the pair (115 of 118 Bill Duels). Second, the male's stab is always directed at the female's face or bill, never at her body. Finally, this behavior is easily recognized by the seesawing action and, in many cases, by the final bill grasping (which resembles a kiss). Virtually everything else varies: duration, number of stabs, relative positions of the mates, feather erections, etc. The male's stabbing is rarely accompanied by the harsh "squawk" vocalizations found in the Forward. And sometimes the female actually returns the stabs instead of just passively recovering.

Many Bill Duels never progress beyond the intention-movement stage of the male standing tall, fluffing out, and feinting a stab. These "face-offs" comprised 23% of the 115 male-initiated Bill Duels in the sample.

(4) *Contexts.*—The great majority of Bill Duels occur during the first few hours that a new pair is together on the nest. At this time the male is still very hostile and seems to be "nervously tolerating" the female who tries to avoid direct confrontations with him. The female keeps her eyes averted most of the time, either poking at twigs or facing away from the male (Fig. 11). She also keeps her crest sleeked and head low: head-raising elicits male attacks more than any other act. Gradually the male ceases his attacks and the female abandons her low-head, facing-away postures. The few female-initiated Bill Duels I saw came at this time, when the intra-pair dominance reached a balance.

(5) *Discussion.*—Bill Duels are highly ritualized if not rigidly stereotyped in form. The orientation of the stab toward the female's face allows her to avoid it easily—without fleeing. Her torso is usually much more vulnerable for serious pecking. By constrast, bachelor males sometimes peck satellite females on the body to drive them away.

The function of the Bill Duel is apparently to reduce the male's attack tendencies and thereby promote peaceful coexistence on the restricted nest-site. The male has to overcome his aggressiveness and the female must overcome her tendency to flee: both goals are attained through these ritualized fights.

Bill Duels are also waged between young siblings starting at about 1 week of age. It is possible that these originate as practice bill-grasping motions like those used for scissor-feeding from the parent's bill.

To my knowledge, elaborate Bill Duels have been described only for Great Blue Herons, Grey Herons (Baerends and van der Cingel 1962), and Cattle Egrets (Blaker 1969a, Lancaster 1970). Adult Cattle Egrets commonly Bill Duel with neighbors from adjacent nests—a situation not observed in Great Blue Herons. I have also seen Bill Duels performed by Great Egrets but they are less common than in the Great Blue Heron.

TABLE 3

RELATIVE FREQUENCIES OF BILL CLAPPERING VARIANTS IN MALE AND FEMALE GREAT BLUE HERONS (DATA FROM TIMELINE SAMPLES)

	Sex of sender			
	Male		Female	
Types of Bill Clappering	N	%	N	%
Aerial	146	25	153	39
Contact	396	67	240	61
Hard Contact	53	9	2	1
Totals:	595		395	

Bill Clappering

I distinguish 3 different forms of Bill Clappering, each of which has been described under various names in the literature: (a) Aerial Bill Clappering—no physical touching occurs between the sender's bill and the receiver's body; (b) Contact Bill Clappering—touching involves only the receiver's feathers; and (c) *Hard* Contact Bill Clappering—the sender's bill is pushed with such force that it passes through the receiver's feathers to the skin.

(1) *Synonyms*:

(a) Aerial Bill Clappering = "clappering" (Huxley 1924), Bill-snapping (Meyerriecks 1960), Bill-clappering (Hudson 1965).

(b) Contact Bill Clappering = mutual preening (Cottrille and Cottrille 1958), Feather-nibbling (Meyerriecks 1960, Baerends and van der Cingel 1962), allopreening (Milstein et al. 1970), *Mordillage* (Voisin 1970), Bill Nibbling (Rodgers in press), low-intensity Back-biting (Blaker 1969a).

(c) *Hard* Contact Bill Clappering = Back-biting (Blaker 1969a, Lancaster 1970).

(2) *Typical performances.*—

(a) Aerial Bill Clappering: The heron starts wagging the tip of its bill from side to side and extends its neck toward the mate (Fig. 12, above). Small nibbling mandibulations (amplitude 1 cm) are performed in mid-air, producing a rapid clicking noise sometimes audible as far as 10 m away. After 1–3 sec the heron retracts its neck to a normal standing position.

(b) Contact Bill Clappering: The heron smoothly extends its neck toward its mate (the lateral head-wags are optional) and nibbles on the mate's feathers (Fig. 12, below).

(c) *Hard* Contact Bill Clappering: The heron pushes its bill forcefully against the mate's body. The bill is usually closed, but lateral head

FIG. 12. Aerial Bill Clappering (above) by male over female's rump as she inserts a nest stick (Hog Island, February 1973). Contact Bill Clappering (below) of feathers on female's neck (Hog Island, February 1975).

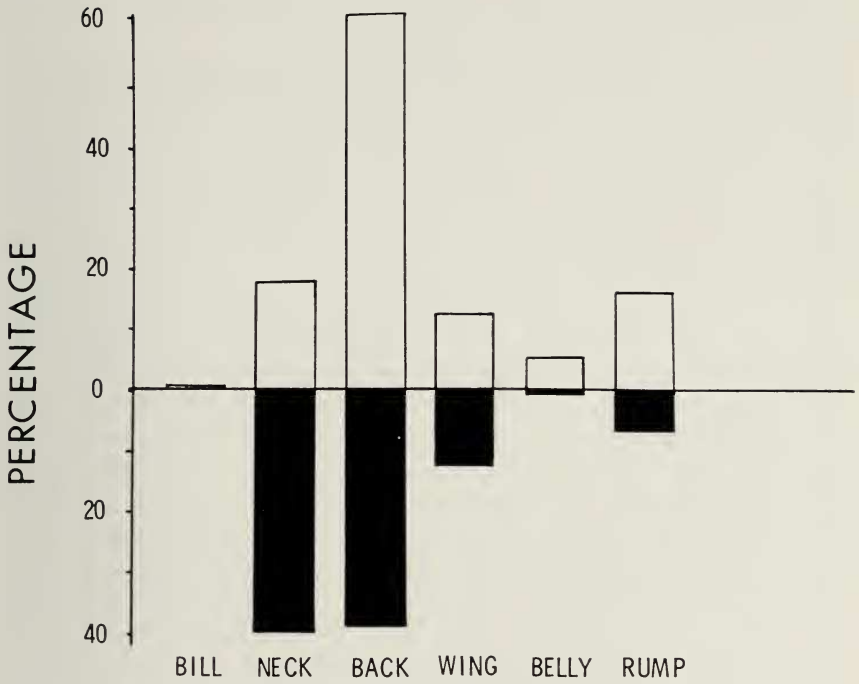

FIG. 13. Regions of the body receiving Contact Bill Clappering from the male (top graph—open bars) and from the female (bottom graph—solid bars).

twists may accompany the physical contact, causing the mate's body to move with the twists. On occasion the receiving bird (who is the female in 96% of my observations) is pushed so hard that it loses its balance and stumbles.

(3) *Variations.*—Contact Bill Clappering is the most common form for both sexes (Table 3), but Aerial Bill Clappering is more important in the female's repertoire than it is in the male's.

Contact Bill Clappering is directed to many different parts of the receiver's body. Males show a marked preference for the female's back while females orient more toward the male's neck (Fig. 13). Most (88% of sample) *Hard* Contact Bill Clappering is directed at the female's back.

Other sources of variability include duration of the display, details of body juxtaposition, body contacts other than the bill during Bill Clappering, and probably speed of mandibulating. On rare occasions a male heron may grasp the female's entire neck while Bill Clappering.

(4) *Contexts.*—Bill Clappering is by far the most common display during the paired stage. It is especially frequent when the mates are first together.

Although Bill Clappering is done by both sexes, males do slightly more (60% of total: data in Table 3) than females.

Bill Clappering may occur any time the mates are on the nest together, but certain activities are more likely to elicit its performance. Sudden movements, sudden changes of behavior, or any action that involves a horizontal neck extension (e.g., Twig Shake, Snap, or inserting nest sticks) often triggers Bill Clappering from the mate. It also occurs sometimes when the receiving mate has done nothing at all (even when it's asleep). Bill Clappering by 1 heron often elicits a Bill Clappering response from the mate: the resulting mutual performance can last up to 10 sec and occasionally ends with the mates' long necks intertwined. It is a common display both preceding and following copulations (as noted for *A. cinerea* by Milstein et al. 1970).

Bill Clappering plays an important role after Bill Duels. As soon as the attacking male ceases his thrusts the female often begins Bill Clappering. This apparently calms the male (his feathers quickly relax) and usually leads to mutual Bill Clappering. On other occasions imminent Bill Duels seem to be replaced by Bill Clappering. When the newly-accepted female elevates her head the male starts to attack but then suddenly Contact Bill Clappers her instead. The female usually reciprocates then and both herons quickly relax. In a similar context, satellite females often perform Aerial Bill Clappering toward a belligerent bachelor male while making the final approaches to his nest. Paired females predictably perform Contact Bill Clappering after their mates direct Forwards at neighbors and passers-by.

Even young chicks perform Aerial and Contact Bill Clappering after hostile events. I elicited this from nestlings at age 2 weeks or older: they first made several volleys of Forwards and then quickly gave mutual Bill Clappering when I backed away.

(5) *Discussion.*—Bill Clappering seems to convey 2 messages, the *non-agonistic* and *bond-limited subsets* (Smith 1969), both of which ultimately strengthen the pairbond. Bill Clappering apparently reduces the male's attack tendencies after he has first allowed a female onto his nest. The female employs 3 behavioral tactics at this time: keeping her head low, directing her bill away from him, and Bill Clappering him frequently (especially after Bill Duels). Second, the signal is used by both sexes to interrupt the mate's other activities, thereby drawing the mate's attention back to the signaller (the *bond-limited* message). For example, a female who is probing among the nest sticks may suddenly receive gentle Contact Bill Clappering from her mate. She immediately stops probing and engages in mutual Bill Clappering for several seconds. In general, Bill Clappering seems to help the pair adjust to the reproductive necessity of coexisting peacefully on a small nest.

Various forms of Bill Clappering have been described for 17 heron species

TABLE 4

SUMMARY OF BILL CLAPPERING HOMOLOGIES IN THE ARDEIDAE

	Aerial	Contact	References
Ardea cinerea	X	X	Hudson 1965
A. herodias	X	X	present paper
A. melanocephala	X	?	Symmes 1951
A. purpurea	X	X	Tomlinson 1974
Casmerodius albus	X	X	Wiese in press, pers. obs.
Egretta garzetta	X	X	Blaker 1969b
E. thula	X	X	Meyerriecks 1960
E. intermedia	X	X	Blaker 1969b
Florida caerulea	X	X	Meanley 1955, pers. obs.
Hydranassa tricolor	X	X	Rodgers in press
Dichromonassa rufescens	X	X	Meyerriecks 1960
Butorides virescens	X	X	Meyerriecks 1960
Bubulcus ibis	X	X	Blaker 1969a
Nycticorax nycticorax	X	X	Nelson 1975
Nyctanassa violacea	X	?	Harford 1951, Nelson 1975
Cochlearius cochlearius	X	X	Mock 1975a
Ixobrychus exilis	X	X	Weller 1961, pers. obs.

(Table 4). Similar mandibulating displays in storks (Up-Down of Kahl, 1972a) and ibises (see review in Hudson 1965) may even be homologous with heron Bill Clappering, but detailed evidence is lacking.

Bill Clappering is a composite display using up to 3 sensory modalities: auditory, visual, and tactile. The acoustic signals of Aerial Bill Clappering are not always audible over distance, especially if there is wind. It is possible that the faintness of this cue is a metacommunicative design feature serving to address the message to the nearby mate only (Bateson 1955, Hockett and Altmann 1968); certainly the tactile components serve this function. The 6 Great Blue Heron chicks that I hand-raised could always be heard when Aerial Bill Clappering at close range.

There are at least 2 plausible, but opposing, explanations for the evolution of Bill Clappering displays. "The Attack-Allopreen Hypothesis" has been presented in bits and pieces before but has not been organized into a comprehensive scheme. The "Autopreen Hypothesis" is new.

The idea that heron allopreening is inhibited attack behavior was first implied by Baerends and van der Cingel (1962) who asserted that Contact Bill Clappering was attack redirected from the mate's body to its feathers. The evolutionary link between inhibited attack and allopreening was developed more fully by Harrison (1965) who specified 2 basic preconditions

that might have been important in the evolution of allopreening in herons: high levels of aggression and enforced close proximity of mates. Hudson's (1965) detailed account of heron Bill Clappering addressed only the final transition from Contact Bill Clappering (allopreening) to Aerial Bill Clappering. He did not speculate on how allopreening itself evolved. Blaker (1969a), however, adopted the "inhibited attack" line of reasoning which he thought contradicted Hudson's allopreening model directly. In fact the 2 ideas are not mutually exclusive but merely represent different stages in the same evolutionary argument.

Thus, according to the synthesized "Attack-Allopreen Hypothesis," selection favored a reduction in the vigor of attack pecking between mates to allow peaceful coexistence on the small nest platform. High levels of male aggression that were advantageous in territorial defense were disadvantageous if unchecked toward females. Because herons are bound by ecological constraints to share parental duties, it is crucial that the mates be able to tolerate each other on the nest. The first evolutionary stage, reduced or inhibited pecking (my *Hard* Contact Bill Clappering), is found in all herons to a greater or lesser extent. In Great Blue Herons it usually lacks the nibbling component and is a relatively infrequent form (only 10% of male, and less than 1% of female Bill Clappering). By contrast, this stage has apparently been favored in the communication system of the Cattle Egret where it is the most common variant (Blaker 1969a).

The second evolutionary stage, gentle Contact Bill Clappering, accordingly reflects continued selection for reduced aggression. This version is directed at the feathers, not the skin, and almost always includes the nibbling component. Nibbling may have been added secondarily as the bill-in-the-feathers position elicited a well-fixed preening response ("transitional action": Lind 1959).

Aerial Bill Clappering may have originated as metacommunication about Contact Bill Clappering, providing the message that "this is going to be ritualized peck-nibble, not an aggressive attack." Examples of similar early warnings being retained as signals themselves are known in monkeys where audible lip-smacking precedes social grooming (Andrew 1963). Alternatively Aerial Bill Clappering could have evolved without metacommunicative function simply as an intention movement to perform Contact Bill Clappering. Here the tactile cues are totally lacking but the mandibulations persist and, without the feathers to muffle them, became more audible. I have observed that Great Blue Herons perceive the differences between Aerial and Contact Bill Clappering and respond differently to these 2 signals.

The opposing "Autopreen Hypothesis" does not have as many obvious selective pressures supporting it. It is based mainly on the observation that

Great Blue Herons, at least occasionally, treat their own neck plumes with ritualized "clappering" that serves no apparent function in feather maintenance. Such performances could be relicts of an early stage in the evolution of Bill Clappering. The "Autopreen Hypothesis" argument is that preening of the neck plumes became ritualized for signal function (as did autopreening of the lead primaries in the case of the Wing Preen) to produce audible clicking sounds. Such a display would serve to maintain acoustic contact between mates and would surely inform the mate of the position and harmless occupation of the bill. Aerial Bill Clappering is the proposed second step, wherein selection favored moving the acoustic signal closer to the mate for better transmission. The addition of tactile cues apparently would have expanded the information content of the display, thus leading to Contact Bill Clappering. Variability in Contact Bill Clappering would provide the raw material for a final selective peak at *Hard* Contact Bill Clappering in those species where more aggressiveness between mates might be advantageous.

The 2 hypotheses thus reflect opposite views of the balance between tendencies for aggression and for closeness. In the "Attack-Allopreen Hypothesis" aggression is considered a holdover from territory defense and an obstacle to proper functioning of the pairbond. But the "Autopreen Hypothesis" envisions aggression as both the ultimate initiator of Bill Clappering evolution and as a secondary adaptive peak in some species like the Cattle Egret.

Advertising Call

Every student of pair-formation behavior in *Ardea cinerea* has described a conspicuous Advertising Call, consistently described as a loud "yelping" call given by unmated males in sporadic volleys from the moment they choose a nest site until the pairbond is formed (e.g., Milstein et al. 1970). There is no controversy over its existence in *A. cinerea*. By contrast, nothing resembling the Advertising Call has ever been described for *A. herodias*, though this species is so closely related to *A. cinerea* that some systematists have proposed lumping the 2 (Parkes 1955, Mayr and Short 1970).

Meyerriecks (1960:101) reported a few observations of Great Blue Heron males in Florida standing on nests and opening and closing their bills, but he was too distant to hear any calls. In 3 field seasons of watching closely for this display in *A. herodias* I have witnessed possible performances on only 3 occasions. These 3 observations are the only times I have seen Great Blue Herons emitting calls not accompanied by any special postures (i.e., not part of a Forward or Stretch). Each heron simply stood on its nest and gave a series of soft, high-pitched "en" vocalizations. The first time (on Hog Island, 1973) 8 irregularly-spaced notes were uttered. The

second observation was made on the same nest the following morning (presumably involving the same male). Then the heron repeated "en" notes irregularly for about 3 min. My third observation (on Hog Island, 1975) consisted of about 8 soft, high-pitched "en" notes, spaced at roughly 1-min intervals. I believe that the true Advertising Call of *A. cinerea* is either totally absent or extremely rare in *A. herodias*. This discrepancy is the most notable repertoire difference yet described for these species.

Special Display Sequences

For the most part, Great Blue Heron displays are not rigidly organized into predictable sequences. This is true both for strings of behavioral events performed by 1 individual and for interactions between 2 herons. Perhaps because of this, heron ethologists have made special note of 3 relatively predictable interaction sequences and have sometimes even described them as displays (which, strictly speaking, they are not). The term "Ceremony" will be used here to connote these sequences.

(1) *Greeting ceremony.*—When 1 heron flies in to join its mate on the nest, it typically gives the Landing Call. The bird on the nest becomes alert and usually performs a full Stretch (less commonly it responds with an Arched Neck or Fluffed Neck) as the arriving mate lands on the rim. Wiese (in press) shows how similar interaction in the Great Egret help the arriving bird find its own nest in the colony: birds whose mates failed to answer the Landing Call tended to alight away from the nest and walk to it. Greeting ceremonies have been described for many herons (e.g., Verwey 1930, North 1963, Blaker 1969a, Rodgers in press, Wiese in press).

(2) *Stick transfer.*—When 1 heron (usually the male) brings sticks to its mate a similar sequence of interactions occurs. The Landing Call is usually omitted, perhaps because most sticks are stolen from nearby nests so the mates never lose visual contact with each other. As the male returns the female does a Stretch (or partial Stretch) then turns and takes the offered stick. Although the male is sometimes reluctant to release his stick he usually does so readily and Bill Clappers the female as she tremble-shoves the new stick into the nest.

(3) *Nest relief.*—During the incubation stage, a special sequence coordinates the mates' actions at changeovers. The arriving heron gives a Landing Call to which the incubating mate stands and performs a full Stretch. After landing nearby the new arrival walks to the nest and finally onto it as its mate exits. Often the pair stands close together for several minutes of Bill Clappering, preening, and even sleeping before the departing mate leaves.

FIG. 14. Pair in simultaneous Tall Alert postures (Hog Island, March 1973).

Miscellaneous Signals

In addition to the easily-recognized displays already described, Great Blue Herons have some less-ritualized behavior patterns that may well convey information.

(1) *Tall Alert.*—When alarmed a Great Blue Heron stands as tall as pos-

sible with bill horizontal, feathers sleeked, and head very still. It seems to rely on its wide peripheral vision to locate the source of the disturbance. This posture serves as a cue to other birds: many neighbors adopt Tall Alert stances even if they showed no overt response to the original stimulus (Fig. 14). Thus the Tall Alert has a social meaning which I believe is unintentional (the heron assuming a Tall Alert is probably trying to gather information for itself: other herons simply use that behavior as a useful piece of information for themselves).

(2) *Shoulder Nibble.*—Great Blue Herons touch their bills to their black epaulet patches from time to time, both between displays and while preening. The act is highly variable, ranging from lengthy nibble-preening to smooth, brief touching (which seems to have no feather-maintenance function and therefore may be a slightly ritualized social signal). No display preening of the epaulets has been described for any heron species to date.

(3) *Treadling.*—Courting male Great Blue Herons sometimes stand on their nests and sway slowly from side to side. This swaying usually takes about 2 sec, is about 20–30 cm in amplitude, and may be accompanied by slight lifting of the free foot with each sway. I do not know the social function of this behavior but it commonly occurs during periods of active displaying and may attract attention to its performer. Similar swaying has been reported for unpaired male Cattle Egrets (Blaker 1969a) and the highly ritualized Snap-Hiss of the Black-crowned Night Heron (Noble et al. 1938, Nelson 1975) may also have evolved from this motor pattern.

(4) *Static-optic Advertising.*—The mere existence of an unmated male heron on his nest-territory carries information to the rest of the colony. Although the Great Blue Heron's signal merely consists of standing, this presence is moderately ritualized in the Cattle Egret (special hunched posture with partial scapular erection: Blaker 1969a) and highly ritualized in the Great Egret (extreme hunched posture with bill pointing down, scapular aigrettes fully fanned: Wiese in press). Despite the simplicity of the posture, the male Great Blue Heron probably transmits a complex *identification* message by his being *on* the nest (unpaired females do not loaf on nests) with his bright-colored softparts and species-typical plumage. His message might be paraphrased as "I am a territory-holding male Great Blue Heron, physiologically ready to breed." Rather than overextend Moynihan's (1955) formal criteria for "display" status, I follow Estes (1969) in calling this type of signal "static-optic advertising."

Fighting

Actual physical combat lasting longer than 1 peck is very rare in Great Blue Heron colonies. Most fights are brief aerial clashes, accompanied by

very loud screams, but producing no injuries. Many seem to result from disputed nest ownership.

Gathering Ground "Dance"

Early accounts of heron breeding behavior often included vague descriptions of herons forming flocks on the ground near the colony and "dancing" (e.g., Bent 1926, Lowe 1954). More recent authors have expressed doubt about the social nature of these aggregations (Baerends and van der Cingel 1962, Milstein et al. 1970, Birkhead 1973).

In March 1971 I watched a group of over 100 Great Blue Herons standing in the snow beside the Rice Lake heronry. Though I watched them for several hours a day during the 4 days before they ascended to the nesting trees, I never saw "dancing." The herons mostly stood still with their heads drawn tightly against their shoulders. The total social activity consisted of occasional Forwards and Arched Necks directed at landing herons.

I believe that those Minnesota herons were merely waiting for environmental conditions to permit colony occupation and nesting. Early migrants are usually confronted with very cold temperatures and almost solidly frozen lakes. For several weeks I saw large numbers of herons scavenging for frozen fish at the lake's melting edge. Others flew long distances toward the Mississippi River and were absent for much of the days. The gathering-ground flocks consistently stayed where weather conditions were most favorable. Several times, when the wind shifted direction, the flock moved to stay on the lee side of the heronry's knoll. The herons spent most of their time standing on 1 foot in the snow with the other foot tucked tightly against the breast feathers.

In the nonmigratory coastal Texas population, breeding is much less synchronized than in Minnesota. Eggs may be found in nests from early January to mid-July (Mock 1975b) with most clutches starting in late February–early March. Accordingly, occupation of the nesting colonies is less synchronous. Some herons can be found roosting in the island colonies at any time of the year, but I have never observed anything like the gathering-ground flocks of northern heronries.

Copulation

Great Blue Heron pairs copulate repeatedly throughout the paired stage and even after 1 or 2 eggs have been laid. I estimate that each pair copulates 10–20 times during this period. A similar estimate of 20 copulations was made by Blaker (1969a) for the Cattle Egret.

I saw no instances of rape (forced copulation with resisting females) or

FIG. 15. Copulation. The female crouches as the male grasps her head and flaps his wings for balance.

extramarital copulations in the Great Blue Herons, either in Minnesota or Texas. Rape has been reported for this species (Cottrille and Cottrille 1958, Michael Brandman pers. comm.), in *A. cinerea* (Verwey 1930) and in 5 other heron species (Taylor 1948, Meanley 1955, Lorenz 1966, Blaker 1969a, Lancaster 1970, Wiese in press), but it seems to be very rare in most herons.

Most copulations occur in the morning and evening hours (females forage away from the colony during midday) and a few occur at night. Every copulation I have seen occurred on the pair's nest, though Cottrille and Cottrille (1958) report that adjacent limbs may be used instead.

As in other herons, little or no overt signaling precedes a Great Blue Heron copulation. Sometimes a male performs Bill Clappering prior to a mounting attempt, but more often he simply walks slowly around the female and steps onto her back. I once saw a successful copulation occur just 10 sec after the male had reared up in an intention-to-Bill-Duel motion.

The male is apparently always on top (see Materials and Methods). He lifts 1 foot and places it gently on the center of the female's back, sometimes raising and lowering the foot several times before finally mounting. For copulation to be successful the female must lean forward and bend her legs slightly. In addition, she holds her wrists a few cm from her sides but not

so far as to form a platform (as reported for *Cochlearius*: Mock 1975a). Uncooperative females do not crouch at all and may continue with some other activity like nest-building. One female turned on her mate and made 4 gentle stabs at him to disrupt a mounting attempt. Once on top the male treadles briefly, grasps the female's humeri with his toes, and lowers himself onto his tarsi. This motion is usually accompanied by wing-flapping for balance. The female moves her rectrices to 1 side and the male wags his lowered tail over the cloaca. The male nearly always grasps the female's head or neck in his mandibles and retains that grip through copulation (Fig. 15). By contrast, male Cattle Egrets rarely hold the female's head (Blaker 1969a) and male Great Egrets never do (Wiese in press).

Sperm transfer presumably occurs when the 2 cloacas are in transitory contact at the midpoint of the male's lateral wags. At the extreme sideways end of the wag the female's cloaca is totally uncovered. Total mount times average about 20 sec, but the 6–10 lateral wags take only about 11 sec and actual cloacal contact is probably less than half of this. Following the final wag the male rises from his tarsal crouch and either steps or flies from the female's back. His departure is often clumsy and may cause the female to stumble.

DISCUSSION AND CONCLUSIONS

Sensory modalities.—So far as is known, Great Blue Herons communicate using only 3 sensory modalities: visual, acoustic, and tactile. Of these, the visual modality is most important. While all 14 described displays have unique and conspicuous visual components (6 are entirely visual), only 6 have acoustic and 4 have tactile components (Table 5). The Great Blue Heron's reliance on visual signals is well suited to its open-nesting habits and diurnality: by contrast, the Boat-billed Heron, which nests in dense mangrove thickets, uses signals that are primarily acoustic (Mock 1975a).

Visual communication has the unique disadvantage of a signal channel that is not permanently open. Visual signals can only reach the intended receiver if that individual is oriented (with eyes open) toward the sender (Wilson 1975). One of the main functions of Great Blue Heron acoustic signals seems to be the maintenance of an open *visual* channel (to draw attention to the performer). This may explain why totally visual signals, like the Wing Preen and Twig Shake, are usually sandwiched into a series of displays that contain acoustic cues. The 3 silent agonistic displays (Fluffed Neck, Upright, and Arched Neck) are employed primarily when the intended receiver is landing nearby and therefore already scanning the area.

Redundancy and multiple functions.—Each message of heron communication is apparently encoded into several different signals (intra-repertoire

TABLE 5

A RANKING OF THE SENSORY MODALITIES OF EACH GREAT BLUE HERON DISPLAY

	Sensory modality*		
	Visual	Acoustic	Tactile
Stretch	1	2	–
Snap	1	2	–
Wing Preen	1	–	–
Circle Flight	1	2	–
Landing Call	2	1	–
Twig Shake	1	–	–
Crest Raising	1	–	–
Fluffed Neck	1	–	–
Upright	1	–	–
Arched Neck	1	–	–
Forward	1	2	3
Supplanting	1	2	3
Bill Duel	1	3	2
Bill Clappering	3	2	1

* 1 = most important, 2 = second most important, 3 = least important, dash = non-existent.

redundancy) and, reciprocally, each signal carries more than 1 message (multiple function: Beer 1975). This redundancy is increased by a high rate of display repetition in many contexts (e.g., a solo male heron may give over a hundred performances of only 6 displays without stopping). Although redundancy and multiple function may in part be artifacts of the ethological units chosen for study, it is likely that both are significant features of heron communication (Table 6).

Redundancy (and repetition) of a message should improve its chances for reaching the intended receivers, especially if they are as mobile as "prospecting" female herons. Furthermore, redundancy allows a message to be expressed in different forms which, by using different sensory modalities, should make it more conspicuous. This signal variety may also help combat habituation in the receiver ("Anti-monotony Principle": Hartshorne 1973). In all these hypothetical ways, redundancy can emphasize those messages which are critical to reproductive success. Someone knowing little about heron courtship would probably predict that the 2 key tasks of an unpaired male are attracting females and defending a nest-territory from other males. Accordingly those functions—male advertisement and nest defense—are served by more displays than any others (Table 6).

TABLE 6

CONTEXTS AND MESSAGES OF GREAT BLUE HERON DISPLAYS

	Displays														
	Stretch	Snap	Wing Preen	Circle Flight	Landing Call	Twig Shake	Crest Raising	Fluffed Neck	Arched Neck	Forward	Supplanting	Bill Duel	Bill Clappering	Tall Alert	Static-optic
I. Uses/Contexts:															
External Disturbances							X	X	X					X	
Nest Defense							X	X	X	X	X			X	X
Male Advertisement	X	X	X	X		X	X								X
Female-female Encounters							X		X	X	X			X	
Greetings at nest*	X				X		X	X	X				X		
Intra-pair Appeasement	X				X								X		
Intra-pair Aggression							X					X			
II. Messages (Smith 1969)															
Identification	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Probability	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
General Set							X								
Locomotion					X	X	X				X				
Attack							X	X	X	X	X	X			
Escape							X								
Nonagonistic	X												X		
Association	X	X	X	X									X		
Bond-limited	X		X		X								X		
Play															
Copulation															
Frustration															

* Includes Greeting Ceremony, Nest Relief Ceremony, and Stick Transfer Ceremony.

The multiple functions feature allows the signal repertoire to remain fairly small (and therefore less ambiguous: Moynihan 1970), without sacrificing content. This multiplicity is possible because the sender's message is usually modified en route by various aspects of the context (Smith 1968, Beer 1975).

Thus the combination of intra-repertoire redundancy and multiple functions can, theoretically, provide an enormous amount of flexibility plus desirable simplicity for a communication repertoire.

SUMMARY

The communication of Great Blue Herons during pair-formation was studied for 4 breeding seasons (2 each) in Minnesota and Texas. Each signal is described for form, variability, and contexts and interpreted for probable functions and evolutionary derivation. An attempt was made to apply the message classification system of Smith (1968, 1969) to heron displays. Six displays are described for the first time in this species. Overall, the communication system of the Great Blue Heron can be characterized as a visual one with acoustic cues serving for reinforcement. Intra-repertoire redundancy and multiple functions of the signals are probably also important.

ACKNOWLEDGMENTS

Financial support for this research is gratefully acknowledged from the Department of Ecology and Behavioral Biology, University of Minnesota (1970–72), Cedar Creek Natural History Area (1970–71), Society of Sigma Xi (1971), National Institutes of Health (Training Grant #5 T01 GM01779 for 1972–76), and the Rob & Bessie Welder Wildlife Foundation (1972–75). Excess page charges were paid by N.I.H. and the Welder Wildlife Foundation.

For assistance in blind construction I thank R. Abraham, J. Ball, C. Barkan, R. Barkley, R. Barrett, S. Derrickson, J. Eldridge, M. Howe, K. Mock, J. Rappole, J. Reagan, W. Reagan, S. Stalheim, and S. Winckler. In addition I wish to thank S. Derrickson, K. Mock, E. Mock, P. Ritner, J. Rodgers, and my advisor, F. McKinney, for editorial criticisms. This paper is contribution number 185 of the Rob & Bessie Welder Wildlife Foundation, Sinton, Texas.

LITERATURE CITED

Andrew, R. J. 1963. The origins and evolution of the calls and facial expressions of the primates. Behaviour 20:1–109.

———. 1972. The information potentially available in mammal displays. *In* Nonverbal Communication (R. A. Hinde, ed.). Cambridge Univ. Press, England.

Baerends, G. P. and J. M. Baerends-van Roon. 1960. Ueber die schnappbewegung des fischreihers (*Ardea cinerea* L.). Ardea 48:136–150.

——— and N. A. van der Cingel. 1962. On the phylogenetic origin of the Snap display in the Common Heron (*Ardea cinerea* L.). Symp. Zool. Soc. Lond. 8:7–24.

Bateson, G. 1955. A theory of play and fantasy. Psychiatr. Res. Rep. 2:39–51.

Beer, C. G. 1975. Multiple functions and gull displays. *In* Function and Evolution in Behaviour (G. Baerends, C. Beer, and A. Manning, eds.). Clarendon Press, Oxford, England.

Bent, A. C. 1926. Life histories of North American Marsh Birds. U. S. Natl. Mus. Bull. No. 135.

Birkhead, T. R. 1973. Observations at a standing-ground adjoining a heronry. Naturalist 924:13–19.

Blaker, D. 1969a. Behaviour of the Cattle Egret, *Ardeola ibis*. Ostrich 40:75–129.

———. 1969b. The behaviour of *Egretta garzetta* and *E. intermedia*. Ostrich 40:150–155.

Bock, W. J. 1956. A generic review of the family Ardeidae (Aves). Am. Mus. Novit. no. 1779.

Cottrille, W. P. and B. D. Cottrille. 1958. Great Blue Heron: behavior at the nest. Misc. Publ. Mus. Zool. Univ. Mich. no. 102.

Daanje, A. 1950. On locomotory movements in birds and the intention movements derived from them. Behaviour 3:48–98.

Darwin, C. 1872. The expression of the emotions in man and the animals. John Murray, London.

Estes, R. D. 1969. Territorial behavior of the Wildebeest (*Connochaetes taurinus* Burchell, 1823). Z. Tierpsychol. 26:284–370.

Harford, H. M. 1951. Nest of the Yellow-crowned Night Heron *Nyctanassa violacea* in Kansas City, Mo. Auk 68:235–236.

Harrison, C. J. O. 1965. Allopreening as agonistic behaviour. Behaviour 24:161–209.

Hartshorne, C. 1973. Born to sing. Indiana Univ. Press, Bloomington.

Hockett, C. F. and S. A. Altmann. 1968. A note on design features. *In* Animal Communication (T. A. Sebeok, ed.), Indiana Univ. Press, Bloomington.

Holstein, V. 1927. Fiskehejren. Gads Forlag, Kopenhagen.

Hudson, M. J. 1965. Bill-clappering display in the Common Heron *Ardea cinerea*. Ibis 107:460–465.

Huxley, J. S. 1924. Some points in the breeding behaviour of the Common Heron. Br. Birds 18:155–163.

Kahl, M. P. 1972a. Comparative ethology of the Ciconiidae. Part 4. The "typical" storks (genera *Ciconia*, *Sphenorhynchus*, *Dissoura*, and *Euxenura*). Z. Tierpsychol. 30:225–252.

———. 1972b. Comparative ethology of the Ciconiidae. The Wood-storks (genera *Mycteria* and *Ibis*). Ibis 114:15–29.

Lancaster, D. A. 1970. Breeding behavior of the Cattle Egret in Colombia. Living Bird 9:167–194.

Lind, H. 1959. The activation of an instinct caused by a "transitional action." Behaviour 14:123–135.

Lorenz, K. 1966. On aggression. Methuen, London.

Lowe, F. A. 1954. The heron. London: Collins New Nat. Monogr., no. 11.

Mayr, E. and L. L. Short. 1970. Species taxa of North American birds, a contribution to comparative systematics. Publ. Nuttal Ornithol. Club no. 9.

Meanley, B. 1955. A nesting study of the Little Blue Heron in eastern Arkansas. Wilson Bull. 67:84–99.

Meyerriecks, A. J. 1960. Comparative breeding behavior of four species of North American herons. Publ. Nuttal Ornithol. Club no. 2.

———. 1962. *In* Handbook of North American Birds (R. S. Palmer, ed.), Yale Univ. Press, New Haven, Connecticut.

Milstein, P. LeS., I. Prestt, and A. A. Bell. 1970. The breeding cycle of the Grey Heron. Ardea 58:171–258.

Mock, D. W. 1975a. Social behavior of the Boat-billed Heron. Living Bird 14:185–214.

———. 1975b. New early egg-date record for Great Blue Herons in Texas. Tex. Ornithol. Soc. Bull. 8:10.

Morris, D. 1956. The feather postures of birds and the problem of the origins of social signals. Behaviour 11:1–12.

Moynihan, M. 1955. Remarks on the original sources of displays. Auk 72:240–246.

———. 1970. Control, suppression, decay, disappearance, and replacement of displays. J. Theor. Biol. 29:85–112.

Nelson, J. B. 1967. Colonial and cliff-nesting in the Gannet. Ardea 55:60–90.

———. 1971. The biology of Abbott's Booby *Sula abbotti*. Ibis 113:429–467.

Nelson, D. 1975. Pair formation behavior of the Black-crowned Night Heron. Honors Thesis, College of Biol. Sci., Univ. of Minnesota, Twin Cities.

Noble, G. K., M. Wurm, and A. Schmidt. 1938. The social behavior of the Black-crowned Night Heron. Auk 55:7–40.

North, M. E. W. 1963. Breeding of the Black-headed Heron at Nairobi, Kenya, 1958–62. J. East Afr. Nat. Hist. Soc. Natl. Mus. 24:33–63.

Owen. D. F. 1959. Some aspects of the behaviour of immature herons, *Ardea cinerea*, in the breeding season. Ardea 47:187–191.

Palmer, R. S. (ed.) 1962. Handbook of North American birds. Vol. I. Yale Univ. Press, New Haven, Connecticut.

Parkes, K. C. 1955. Systematic notes of North American birds. 1. Herons and ibises. Ann. Carnegie Mus. 33:287–293.

Percy, Lord W. 1951. Three studies in bird character. Country Life, Ltd. London.

Portielje, A. F. J. 1926. Zur ethologie bezw. psychologie von *Botaurus stellaris*. Ardea 15:1–15.

Pratt, H. M. 1970. Breeding biology of Great Blue Herons and Common Egrets in central California. Condor 72:407–416.

Rodgers, J. A., Jr. Breeding displays of the Louisiana Heron. Wilson Bull., in press.

Selous, E. 1927. Realities of bird life. Constable & Co., Ltd. London.

Smith. W. J. 1968. Message-meaning analysis. *In* Animal Communication (T. A. Sebeok. ed.). Indiana Univ. Press, Bloomington.

———. 1969. Messages of vertebrate communication. Science 165:145–150.

Strijbos, J. P. 1935. De Blauwe Reiger. L. J. Veen, Amsterdam.

Symmes, T. C. L. 1951. Display of the Black-necked Heron. Ostrich 22:38.

Taylor, J. S. 1948. Notes on the nesting and feeding habits of *Ardea melanocephala*. Ostrich 19:203–210.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae) : a progress report. Behaviour 15:1–70.

Tomlinson, D. N. S. 1974. Studies of the Purple Heron, part 2: behaviour patterns. Ostrich 45:209–223.

Verwey, J. 1930. Die paarungsbiologie des fischreihers. Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere. 48:1–120.

Voisin. C. 1970. Observations sur le comportement du heron bihoreau *Nycticorax n. nycticorax* en periode de reproduction. Oiseau 40:307–339.

Weller, M. W. 1961. Breeding biology of the Least Bittern. Wilson Bull. 73:11–35.

White. S. J. 1971. Selective responsiveness by the Gannet to played-back calls. Anim. Behav. 19:125–131.

———, R. E. C. White, and W. H. Thorpe. 1970. Acoustic basis for individual recognition in the Gannet. Nature 225:1156–1158.

Wiese, J. H. 1976. Courtship and pair formation in the Great Egret. Auk. in press.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Belknap/Harvard Univ. Press, Cambridge, Massachusetts.

J. F. BELL MUSEUM OF NATURAL HISTORY, UNIV. OF MINNESOTA, MINNEAPOLIS 55455. ACCEPTED 15 MAR. 1976.